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FIG. 1—A terminal shoot of a potato plant affected with purple-top wilt showing the characteristic upward rolling of the leaflets. The rolling is more pronounced at the base of the leaflets. The rolled portion of the leaflet assumes a purplish tinge in pigmented varieties and is pale yellow in varieties lacking red pigment. (Enlarged print from a Kodachrome transparency.)

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INTRODUCTION

A destructive disease of potatoes commonly known as "purple-top wilt" or "blue stem" has been prevalent in West Virginia since 1931. It has been reported also from several other states but appears to be most abundant in the northern and eastern part of the country, the range of its greatest prevalence being from New York State westward to Minnesota and North Dakota and southward through the mountainous areas of Pennsylvania and West Virginia. It has not been reported to be of any importance in the southern states nor in the Far West.

The disease is probably not new, but it evidently was not observed in abundance before 1930. When only an occasional plant is affected, purple-top wilt is easily confused with Rhizoctonia injury, certain types of Fusarium wilt, or any one of several virus diseases. However, when it became so prevalent that more than half of the plants in a field were affected, it was soon recognized as a disease different from any previously described.

One of the earliest published references to the disease is that of Muncie (*16*), who in 1931 published a brief description of a disease which he called the "moron" disease, stating that this nondescriptive name had been applied to it in 1925. In a later note (*17*) it is stated that the disease had been observed in Michigan since 1915. Photographs and more complete descriptions obtained by correspondence clearly identify this disease with purple-top wilt. The senior author recalls having observed the disease in Minnesota as early as 1921, when it was commonly diagnosed as a secondary symptom of Rhizoctonia stem rot. In 1935 the disease became very prevalent in Minnesota and was tentatively diagnosed by Leach and Darling (*10*) as atypical Fusarium wilt. Further observations and extensive inoculation experiments reported by Leach and Decker in 1938 (*11*) failed to confirm this diagnosis and pointed to an insect relationship. Similar symptoms were produced by experimentally feeding tarnished plant bugs on caged plants in the greenhouse, but later and more extensive experiments by Leach (*12*) in 1939 distinguished this injury from true purple-top wilt and eliminated this insect as a possible agent or vector. This and further work with possible insect vectors led to the conclusion that the disease referred to as "purple-top wilt" was transmitted by the aster leafhopper (*Macrosteles divisus* (*Uhl.*) and was probably caused by the aster-yellows virus (*Chlorogenus callistephi* Holmes).

The most complete description of the disease was published in 1937 by Orton and Hill (*18*), who had observed the disease in West Virginia since 1931. Their description clearly identifies the West Virginia disease with the one prevalent in Minnesota and Michigan. In the following year Orton and Hill (*19*) applied the name "blue-stem" to the disease because of the characteristic discoloration of the stem on the Rural variety. In that paper they also presented evidence indicating that it was initiated by some unknown insect. In the same year Hill and Orton (*5*) and Hill (*6*) published extensive microchemical and histological studies of tubers from affected plants. Further evidence supporting the conclusion of Leach (*12*) that purple-top wilt is caused by the aster-yellows virus was presented by Younkin (*24*) in 1943.

The purpose of this bulletin is to summarize the known facts about the disease and to present the results of investigations carried out in West Virginia since 1939.

FIG. 2—A potato plant showing early stages of infection with purple-top wilt. Note cessation of apical growth and excessive development of axillary shoots. At this stage the leaves are turgid, and there is no indication of wilt. The abnormal purple pigmentation is most pronounced at this stage.

SYMPTOMS

The most important symptoms of the disease as it occurs in West Virginia have been described by Orton and Hill (*18*). The first symptoms appear only after the plant is well developed and are rarely observed before the middle of July, when tuberization is already well under way. The earliest symptoms are found on the immature terminal leaflets which do not expand normally but roll upward, especially near the base (Fig. 1). There is noticeable cessation of terminal growth of the affected shoot (Fig. 2). This condition is accompanied by abnormal discoloration. In all pigmented varieties the rolled leaflets assume a purplish color, the intensity varying with the variety and certain environmental conditions. It is most pronounced in the Triumph variety and is entirely lacking in such varieties as Green Mountain, which normally lack pigment. In these varieties, however, the leaflets become chlorotic and assume a pale yellow color. All intermediate gradations between these two extremes may be found on the commonly grown varieties. In the Rural variety there is a corresponding intensification of the normal purple or blue color of the stem, but this symptom does not occur on most other varieties.

Affected leaflets are at first more rigid and somewhat leathery, and the petioles are abnormally brittle. Later, however, the leaves wilt and be-

FIG. 3—A potato plant with one shoot affected with purple-top wilt and with two others remaining healthy. A more advanced stage of the disease than that shown in Figure 2. Here the affected shoot has begun to wilt. The frequency with which one or more of the shoots from a single seedpiece become affected while the others remain healthy is additional evidence that the disease is not perpetuated in the tubers like other virus diseases affecting potatoes.

FIG. 4—Two shoots from a potato plant affected with purple-top wilt showing axillary shoots with swollen bases forming incipient aerial tubers. Some leaves have been removed to show the axillary shoots more plainly. These symptoms occur only when plants are growing under conditions of optimum temperature and sunlight.

come flaccid. Shortly after the terminal leaflets are affected there is abnormal development of shoots from the axillary buds. There may be an almost complete loss of apical dominance (Fig. 2), but the axillary shoots soon develop the same symptoms that occur on the terminal shoot and do not develop very long before the entire affected stem begins to wilt (Fig. 3). If infection takes place early, before tuberization has advanced too far, the starch will be stored in the bases of the axillary shoots, often producing well-developed axillary tubers (Fig. 4). On plants affected late, or in very hot weather, when there is no surplus of photosynthetic products, this symptom may be entirely lacking. Axillary tubers have never been observed on artificially inoculated plants grown in the greenhouse, where photosynthetic activity is subnormal.

Within ten days or two weeks after the first symptoms appear the affected shoots invariably wilt and may die within a few days. Under certain conditions, however, they may remain alive for a long time. After heavy rains the axillary shoots on wilted stems may show signs of renewed growth. In some cases affected plants may continue growth after normal plants have matured. When such plants are subjected to early frosts they may be distinguished from the healthy plants by the more intense black color of the frozen stems as compared with the light brown stems of the mature healthy plants. This tendency of affected plants to remain alive longer than healthy plants has been reported by Kunkel (*7*) for several virus diseases including aster yellows.

When wilting stems are examined, a pronounced necrosis of the vascular bundles at or near the ground line is always present (Fig. 5). This condition closely resembles symptoms of Fusarium wilt, with which the disease is frequently confused. In fact, species of Fusarium often invade the vascular elements and can be isolated from such stems. Leach and Decker (*11*), however, made extensive inoculations with cultures isolated from affected stems and proved that they were secondary and not the cause of the disease.

FIG. 5—Four potato stems split at the base near the point of attachment to the seedpiece. The two stems on the left were affected with purple-top wilt and show the characteristic necrosis of phloem and adjacent tissues. The two stems on the right are healthy.

In West Virginia this necrosis regularly extends through the stolons into most of the tubers on affected plants, causing a characteristic brown stem-end discoloration (Figs. 7 and 8). The necrotic stolons separate from the tubers in a characteristic manner, leaving a prominent cavity at the point of attachment (Fig. 6). The necrosis in the tubers is most extensive in the vascular elements, but it may extend into the storage parenchyma also. Although fungi often may be isolated from this necrotic tissue they are secondary invaders. The necrotic areas are frequently sterile and, since they are soon walled off by a layer of wound cork, affected tubers do not appear to be any more subject to decay in storage than normal ones.

This stem-end discoloration of tubers is almost universal in West Virginia, but it is not a constant symptom of the disease as it occurs in Minnesota. The senior author studied the disease there for several years, and, although vascular necrosis of the bases of affected shoots was a constant symptom, the necrosis did often extend far into the tubers. No satisfactory explanation for this difference in symptoms in the two regions can be given, but it is believed to be due to differences in environmental conditions. In all other respects the symptoms agree very closely in both localities.

Muncie (*16*) in describing the "moron" disease in Michigan points out that "at least one, or often more, of the tubers are flabby." Soft, flabby tubers are often found on affected plants in Minnesota and have been observed occasionally in West Virginia. They are, however, much less common in West Virginia than in Minnesota.

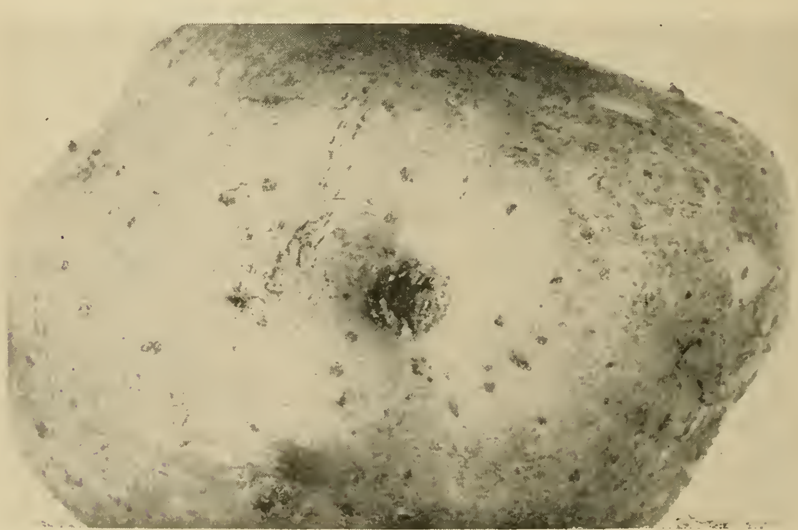

FIG. 6—The stem end of a tuber from a plant affected with purple-top wilt, showing the characteristic necrotic tissue at the point of attachment of the stolon.

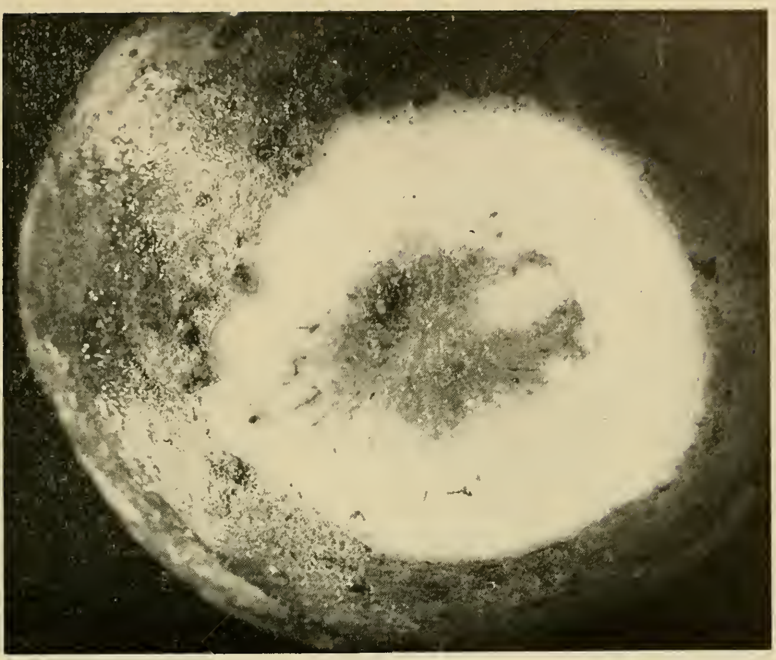

FIG. 7—A tuber such as that shown in Figure 6 cut in cross section about one-fourth inch from stem end. Note the characteristic browning of vascular elements and adjacent tissue.

OTHER DISEASES WITH WHICH PURPLE-TOP WILT HAS BEEN OR MAY BE CONFUSED

The symptoms of purple-top wilt are not sufficiently specific to prevent one who has not made a special study of the disease from confusing it with certain other diseases. As previously mentioned, before it was recognized as a specific disease, it was often diagnosed as a secondary symptom of Rhizoctonia stem rot. In later stages of development it was sometimes confused with Fusarium wilt. Muncie (*16*) mentioned its similarity to certain types of blackleg infection in which the bacterial decay is confined mostly to the pith and is not obvious. Since the most prominent vine symptoms are the result of accumulation of elaborated foods in the vines in consequence of faulty translocation, it is not strange that similar symptoms should result from any disease that interferes with translocation of the products of photosynthesis without immediately killing the plant. The writers have, in fact, observed vine symptoms almost identical with those of purple-top wilt caused by mechanical injury that severed the phloem tissues during a period of high photosynthetic activity without interfering with the xylem vessels. They also have observed strikingly similar symptoms caused by blackleg infection under very humid conditions. The similarity in such cases, however, persists for only a short time.

McLean (*15*) has reported a wilt of potatoes in Wisconsin (said to be caused by *Fusarium avenaceum*) for which the symptoms were reported as follows: "There is a reduction of leaf area due to the decrease in size of the leaflets on apical leaves and an increase in the number of folioles. The axillary buds are stimulated into production of secondary shoots or aerial tubers. Clorosis and tipburn are typical along with rigidity of stem and petiole. The leaves roll upward and produce a harsh texture. Reddening or purpling of the tops is not uncommon." The symptoms of this disease are obviously similar to those of purple-top wilt, and the two might easily be confused.

When the disease was first recognized by the senior author in Minnesota, it was tentatively diagnosed as a Fusarium wilt because a species of Fusarium was readily isolated from the necrotic vascular elements of the lower stems. But it was later observed that, when diseased plants were growing on peat soil, the necrotic bundles were present but were never invaded by Fusarium. Later inoculation experiments (*11*) demonstrated that the Fusarium so observed and isolated was a secondary invader.

Several virus diseases have been reported with symptoms resembling those of purple-top wilt. When purple-top wilt was first recognized in Minnesota in 1935, several observers diagnosed it as "hay wire," a disease under observation in Nebraska at that time. A closer comparison of

FIG. 8—A tuber similar to the one shown in Figure 7 cut in longitudinal section through the stem end showing the extension of browning along the vascular ring.

these two diseases revealed a number of differences, the most important of which was the tuber transmission of "hay wire" and its occurrence on very young plants—two things that never occur in purple-top wilt. These facts: namely, the absence of tuber transmission of purple-top wilt and the absence of symptoms on young plants, are not fully appreciated by those who have not studied the disease carefully.

Another disease with symptoms strikingly similar to those of purple-top wilt was described by Sanford and Clay (*20*) as "purple dwarf" with symptoms as follows: "Apical growth is checked, the entire plant becomes stunted, the newer leaves develop a purplish hue along their margin and curl upwards, the phloem of the entire plant is disorganized and a well developed, brown, dendritic necrosis extends from the proximal to distal ends of the tuber. First the roots, then the stolons, and later the base of the stem become brown and decay." However, Sanford and Clay point out that the disease is perpetuated through the tubers, and plants from diseased tubers show symptoms as soon as they emerge from the ground. Purple dwarf is not only transmitted through tubers but is also transmitted to healthy plants by grafting. These characteristics clearly distinguish purple dwarf from purple-top wilt, although the major symptoms are very similar.

Severe outbreaks of a condition known as "stem-end browning" of potato tubers have been reported from Maine (*3*). This condition resembles in many respects the stem-end necrosis often associated with purple-top wilt. It, however, has not been associated with the vine symptoms of purple-top wilt and is probably due to some other cause.

It should be recognized that the symptoms associated with purple-top wilt are not restricted to this disease and, since no visible parasite is present, its diagnosis is not a simple matter. Diagnosis is made still more difficult by our inability to recover the virus from affected plants. Accurate diagnosis of purple-top wilt from a single isolated specimen is not easy. However, when it is very prevalent and when its development can be watched throughout the season, no great difficulty is experienced. In diagnosing the disease and in distinguishing it from diseases with similar symptoms the following points are of prime importance:

First, it is not tuber-transmitted and is never found on young plants; the first symptoms appear at or after blossoming time.

Second, the plants always wilt within two or three weeks after appearance of symptoms.

Third, there is always a necrosis of the vascular elements at the base of the stem, often but not always extending into the stem end of the tubers.

Fourth, translocation is inhibited and there is accumulation of carbohydrates in the vines. The other associated symptoms, including abnormal purple pigmentation and production of aerial tubers, may vary with variety, light intensity, temperature, and many other factors.

ECONOMIC IMPORTANCE

It is difficult to measure the economic loss caused by purple-top wilt and few attempts have been made to estimate it. Orton and Hill (*19*) recognized it as the limiting factor in potato production in some areas in West Virginia. Its prevalence may vary in regions of general occurrence from a few scattered infected plants in certain fields to nearly 100 percent infection in others. The degree of reduction in yield depends not only upon the number of infected plants but also on the time of infection. The disease is rarely found before tuberization is well under way, and the percentage of infected plants increases progressively until the plants are mature or until they are killed by frost. The yield of the earlier-infected plants is reduced more than half, but the yield of later-infected plants may be reduced only slightly. Under average conditions 100 percent infection would probably cause a reduction in yield of no more than 50 percent. Because the disease normally appears late in the season, the reduction in yield is greater in late varieties or in late-planted fields than in early varieties or in early planted fields. In fact, varieties such as Irish Cobbler mature so early as to suffer very little injury from the disease in West Virginia. This is not true in northern Minnesota and neighboring states, where even the early varieties do not mature early enough to escape infection. However, in certain areas in these states, when early varieties are planted on light soils and harvested *before* complete maturity, the disease is of little or no economic importance.

Even though the yield may not be greatly reduced, there may be much greater decrease in quality. In West Virginia, and in neighboring states where stem-end necrosis of tubers is a constant symptom of the disease, reduced quality is more serious than the reduction in yield. As pointed out by Orton and Hill (*19*), "the housewife seriously objects to the use of local potatoes because of tuber necrosis," and "in many markets it is difficult to sell locally produced table stock. At the same time fancy prices are being paid for introduced table stock." Farther north this factor is not so important because the stem-bud discoloration is not always associated with affected plants.

The economic importance of the disease is limited by the fact that it, unlike other virus diseases affecting the potato, is not transmitted through the tubers. If it were tuber-transmitted, it would cause much more damage than it does. However, as will be pointed out in more detail later, even though the disease is not transmitted through the tubers, badly affected tubers produce plants with less vigor than do tubers from healthy plants.

Long (*14*) in 1935 published a brief note to the effect that the condition known as "spindling sprout" or "hair sprout" is associated with purple-top wilt and is found on tubers from plants affected with purple-top wilt and not on tubers from other plants. The writers have not been able to confirm this conclusion. Over a period of several years hundreds of tubers from affected plants have been selected for observation and study. Although such tubers produced sprouts weaker than those produced by tubers from healthy plants, no true hair sprouts have ever been observed on them. Also, when true hair-sprout tubers were planted, they produced weak plants, but they manifested no symptoms of purple-top wilt. All available evidence indicates that the two diseases are distinct and different.

ETIOLOGY

The nature and cause of purple-top wilt has been difficult to determine. Observations and experiments by Orton and Hill (*19*) and by Leach and Decker (*11*) pointed clearly to insect relationship and probable virus origin, but the absence of tuber transmission, a characteristic of all previously known virus diseases affecting potatoes, obscured the problem. Inasmuch as the disease was not perpetuated in the tubers, it could be studied directly only during the short period of its development on field-grown potatoes. Leach (*12*), working in Minnesota, experimentally produced the disease on caged plants by means of the aster leafhopper and concluded that it was probably caused by the aster-yellows virus. However, absence of tuber transmission of the virus and failure to transmit the virus from potato to asters made further work necessary before final conclusion could be reached. Since 1939, study of the disease has been continued in West Virginia, and sufficient evidence has been obtained to justify the conclusion that purple-top wilt is caused by the aster-yellows virus and is transmitted by the aster leafhopper, *Macrosteles divisus* (Uhl.).

Although Kunkel (*6*) in his extensive study of the host range of the aster-yellows virus was unable to obtain infection on the potato, Severin and Haasis (*21*) successfully inoculated potatos with the California strain of the virus. The symptoms as described by these authors were strikingly similar to those of purple-top wilt. Severin (*22*) also has reported finding in California a single potato plant with purple leaves and aerial tubers from which he was able to recover the aster-yellows virus by means of a long-winged strain of *Macrosteles divisus.* According to Severin (*23*) the disease is of no economic importance on potatoes in California.

Inoculation experiments:—Each year from 1939 to 1943 inclusive, from 40 to 60 aster-cloth or screen-wire cages (Fig. 9), enclosing 4 to 6 potato plants, have been used for field inoculation experiments with aster leafhoppers and certain other insects as possible vectors. It will not be necessary to describe each of these experiments in detail. In all the experiments no plant developed the disease in a cage in which aster leafhoppers were not introduced, while the disease appeared in 18.9 percent of the 290 cages in which aster leafhoppers were introduced. This is a relatively small percentage of successful infections, but in some of the cages the hoppers were caught in the field on various plants and were not known to be viruliferous. Others were introduced too late in the season to allow for the long incubation period now known to be necessary. When known viruliferous leafhoppers were used, the percentage of success was much higher; approximately 40.8 percent in a total of 98 cages.

The symptoms produced on caged plants were similar in all essential characters to those on plants naturally infected. However, it should be

FIG. 9—Two rows of aster-cloth cages of the type used in field inoculation experiments.

stated that there were some minor differences. These can probably be explained by the reduced light intensity and the slightly higher temperatures in the cages. The terminal leaves were less rigid and the pigmentation less intense than those of corresponding non-caged plants. Axillary shoots were less inclined to be thickened at the base, and axillary tubers were rarely present. The stem-end necrosis of tubers, although present, was usually less pronounced on caged plants. Since the foliage symptoms, including coloration and rigidity, are closely associated with accumulation of photosynthetic products in the vines, these differences are believed explainable by reduced light intensity in the cages and by a corresponding lowered photosynthetic activity. The yields of both diseased and healthy plants under the cages were always lower than those of corresponding non-caged plants.

During the winter months similar experiments were made in the greenhouse. Viruliferous leafhoppers taken from affected aster plants were allowed to feed on potato plants under various conditions. Transmission of the virus and production of definite symptoms, although erratic, were successful in almost 50 percent of the experiments. Under the poor light conditions prevailing in Morgantown in winter, potatoes do not grow well in the greenhouse especially when confined in cages where light is further reduced and where temperature tends to rise excessively when the sun shines. Under such conditions photosynthetic activity is low, respiration is abnormally high, and growth is spindly. Potato plants affected with the aster-yellows virus under these conditions, like those in field cages, present a set of symptoms which in some minor respects vary from those observed on plants in the field (Figs. 10 and 11). Many inoculation experiments made in spring and early summer gave negative results that could be explained only by the high temperatures which prevailed and which could not be avoided in the greenhouses at that season of the year. Kunkel (*9*) has shown that viruliferous leafhoppers soon lose their ability to transmit this virus at temperatures above 31°C., a temperature that cannot be avoided in most greenhouses on bright sunny days in late spring, summer, and early fall. Better results and more typical symptoms were obtained when more favorable greenhouse temperatures were provided by automatic ventilator control, thus eliminating the occasional periods of excessively high temperature, and when the plants were provided with supplementary light from daylight fluorescent lamps.

In the later years most of the inoculation experiments made in the spring and summer were made in a 10x12 ft. screen-wire house with walls of 16-mesh screen and a glass roof. In this structure, located so that it was partly shaded during the hottest part of the day, temperatures were not appreciably different from outside temperatures, and periods of excessively high temperature were avoided.

Some greenhouse experiments were inconclusive because of the long incubation of the virus in potatoes. Often the potato plants would be

FIG. 10—Three potato plants experimentally inoculated with the aster-yellows virus and a healthy check plant. Viruliferous leafhoppers were fed on young potato shoots for 10 days, then removed. The experiment was carried out in the greenhouse during January and February. Two of the plants have already begun to wilt.

showing changes associated with normal maturity under the conditions of growth before completion of the incubation period. In later experiments a higher percentage of success was obtained by greensprouting the seed pieces and subjecting them to viruliferous leafhoppers before planting.

Making allowance for certain of the early failures due to the causes mentioned, 48.5 percent of the inoculations made in the greenhouse or in the screen-wire house with known viruliferous leafhoppers were successful. The results of these inoculation experiments together with those made in the field are considered sufficient to justify the conclusion that purple-top wilt is caused by the aster-yellows virus, although its behavior in the potato plant is different from that in aster. The result of the inoculations reported here agree rather closely with those of Younkin (*24*) who studied the disease in New York. He found transmission of the virus to potatoes to be erratic but obtained successful transmission in 43.8 percent of the plants inoculated with a strain of the virus obtained from ragweed *Ambrosia artemisiifolia*).

The prevalence of leafhoppers in potato fields:—During the course of the work numerous experiments were made in which leafhoppers caught in the field on various plants in the vicinity of potato fields were used. In these experiments a much lower percentage (approximately 4%) of infection resulted. In view of the relatively low percentage of successful infection produced in artificial inoculation with insects taken from the field, it is not easy to account for the high percentage of infection that

FIG. 11—The upper parts of one of the plants shown in Figure 10. Note the upward rolling of the leaflets of the spread leaves and the development of axillary shoots. The characteristic purple pigment was present in curled leaflets.

so frequently occurs in nature. This is especially true when we consider the fact that the potato is not a preferred host of the aster leafhopper and that they are usually present on potatoes in relatively small numbers as compared with the *potato* leafhopper, which breeds abundantly on potatoes.

For three successive years, 1941-1943 inclusive, prevalence of the leafhoppers in an experimental potato field was determined by making uniform sweeps with an insect net and counting the insects caught. A wide variety of insects was caught, many of which occurred in small numbers and were not identified. Of particular interest are the relative numbers of the aster leafhopper and of the common potato leafhopper (*Empoasca fabae Harris*). Beginning in early June, from 2 to 40 specimens of each species would be caught in each sample. Before the end of June the potato leafhoppers became very numerous, the sample usually yielding several hundred. The numbers of aster leafhoppers caught, however, remained relatively constant, rarely exceeding 40 in any one sample. This relationship is shown in Table 1.

TABLE 1—Relative Abundance of Aster and Potato Leafhoppers in Potato Fields as Indicated by Uniform Sample Sweepings Made with a Standard Insect Net in 1941, 1942, and 1943

1941			1942			1943		
Date	Aster leaf-hoppers	Potato leaf-hoppers	Date	Aster leaf-hoppers	Potato leaf-hoppers	Date	Aster leaf-hoppers	Potato leaf-hoppers
June 10	2	10	June 3	2	40	June 10	20	20
June 17	8	24	June 11	20	80	June 18	23	30
June 24	25	116	June 17	35	90	June 25	15	130
July 2	110	170	June 30	20	173	July 2	25	142
July 10	35	200+	July 10	15	200+	July 10	40	160
July 16	20	200+	July 13	12	250+			

Among the insects caught occasionally on potato plants and often in light traps was the black-face leafhopper, *Thamnotettix nigrifons* Forbes. It was thought that this leafhopper might be transmitting a virus to potatoes. Therefore extensive inoculation experiments were made on potatoes and asters. Insects caught in the field were used as well as those fed on aster plants affected with yellows or on potatoes affected with purple-top wilt. In no case was evidence of virus transmission obtained. It was concluded that *Thamnotettix nigrifons* is not a vector of purple-top wilt.

THE VIRUS FROM WEEDS COMPARED WITH THE VIRUS FROM ASTERS:—It was thought that perhaps a distinct strain of the aster-yellows virus might be responsible for the disease on potatoes and that, if it could be found, a higher percentage of infection could be obtained. A search was made in the vicinity of potato fields for weeds affected with a virus disease resembling aster yellows. Ragweed (*Ambrosia artemisiifolia* L.) was the most commonly found plant showing such symptoms. A few plants of Erigeron spp. and wild lettuce (*Lactuca scariola*) were observed. When attempts were made to transmit the virus from these plants to potatoes it was not transmitted any more readily than the strain obtained from asters.

It was observed that aster leafhoppers were very numerous on plantain (*Plantago major* and *Plantago minor*) in early fall after potato harvest. Some of these plants appeared abnormally chlorotic; since they had been reported as being susceptible to the aster-yellows virus, they were suspected of being infected. However, leafhoppers fed upon these plants did not transmit the virus to potatoes or to asters.

Failure to transmit the virus from potatoes:—Although the virus of aster yellows has been transmitted to the potato by the aster leafhopper, all attempts to transmit the virus from potatoes to asters have failed. For three successive years, beginning with the first appearance of the disease in the field and continuing until no naturally infected potatoes were available, non-viruliferous aster leafhoppers were fed on potato plants affected with the disease and then transferred to aster plants. In some experiments the hoppers were placed in celluloid cages on infected shoots in the field and, after feeding for various lengths of time, were removed and placed on aster plants. In other experiments, because of the high temperatures prevailing in the fields, naturally infected shoots were cut and the stems placed in flasks of water or in wet sand and removed to a cool place where the leafhoppers were allowed to feed. When the leafhoppers were removed from infected potato plants, from 4 to 12 insects were placed on a healthy aster plant under a ventilated celluloid cage (Fig. 12). After feeding for a period of three to five days on the aster plants they were removed to new plants, and the process was repeated until more than ample time for the incubation period in the insect had elapsed. In all, 118 aster plants were inoculated with leafhoppers which had fed on naturally infected potato plants. Only negative results were obtained. In a similar manner 11 aster plants were inoculated with leafhoppers which had fed on potato plants artificially inoculated with the aster-yellows virus. Here also only negative results were obtained.

During the first year the aster plants were kept in the field or in a greenhouse where the temperature at that time of the year often reached the danger point for transmission of the virus. Failure to transmit the virus under these conditions led to the hypothesis that the failure might be caused by the high temperatures. Kunkel (*9*) has shown that transmission of the virus from asters to asters is greatly reduced at temperatures of 31°C. or higher. He reported that the disease spread in nature much more slowly in the hot weather of midsummer than it did in the cooler weather of late spring and early fall. For this reason during the next two seasons aster plants used in inoculation experiments were kept either in the outdoor screen-enclosed structure or in the window of a cool basement room. Control inoculations were made at the same time with the virus on asters in which the virus was readily transmitted from asters to asters. It is evident therefore that failure to transmit the virus from potatoes to asters was not due to the high temperatures at the time of feeding the leafhoppers.

FIG. 12—A small ventilated celluloid cage used in inoculating young potato shoots and aster plants by means of viruliferous leafhoppers.

Severin (*22*) in California has reported the recovery of the aster-yellows virus from a single potato plant found naturally infected. This was accomplished by using a strain of *Macrosteles divisus* referred to as the long-winged strain. This strain of the aster leafhopper, insofar as the writer has been able to determine, does not occur in West Virginia. It is possible that some method for readily recovering the virus from potato may be found by further study, but the authors have been unable to do it.

Younkin (*24*) also was not able to transmit the virus from potatoes to asters by leafhopper feeding, but he reported transmission by grafting scions from affected potato plants to *Nicotiana rustica* in 4 out of 198 grafts. The virus obtained in this way was transmitted by leafhoppers from *N. rustica* to asters on which typical symptoms of aster yellows were produced.

The authors have made numerous attempts to recover the virus from naturally infected potatoes by this method but have not been successful. Similar attempts to transmit the virus from potato to potato were also unsuccessful. It was difficult to obtain a successful graft using a scion from a plant affected with purple-top wilt, but union was obtained in 7 cases. In none of these was definite proof of transmission obtained.

Perpetuation of virus in potato cuttings not successful:—Numerous attempts were made to perpetuate the virus by making cuttings from infected plants. Cuttings were taken from various parts of affected shoots as soon as definite symptoms appeared. These were handled in various ways including treatment with root-stimulating hormones and planted in wet sand in a moist chamber. Several hundred cuttings were planted under a variety of conditions, but not a single successful propagation was obtained. In a few cases a few roots were formed, but the shoot failed to become established and did not grow long enough to develop any symptoms of the disease. Cuttings from healthy plants were made at the same time and, although not all of these were successful, many rooted and grew normally. It is evident from these experiments that the disease affects the physiology of the plant so that normal graft unions and cuttings can be obtained only with great difficulty if at all.

Virus not transmitted through potato tubers:—It was recognized early that purple-top wilt is not tuber-transmitted. Before the virus nature of the disease was proved, Leach and Decker (*11*) made extensive experiments with hill and tuber-unit plots using healthy plants and plants affected with purple-top wilt. In these experiments and in similar experiments carried out in West Virginia in later years the number of infected plants was not significantly greater in the plots planted with tubers from purple-top wilt plants than in those planted with tubers from healthy plants. In a preliminary experiment 456 plants from tubers selected from diseased plants were grown in hill and tuber units in comparison with 230 plants from tubers from healthy plants. Sixteen percent of the former developed purple-top wilt, while only 9 percent of those from healthy plants were affected. This experiment might at first glance be interpreted as indicating some tuber transmission, but similar experiments in subsequent years did not support the conclusion. Moreover, there was no relationship between tuber or hill units and the occurrence of the disease. Often only one plant in a tuber unit of four or more seedpieces would show the disease, and in no case were all plants of a tuber unit affected. The same lack of correlation between tuber and hill units was obvious. The frequency with which only one of two or more plants arising from the same seedpiece became affected is strong evidence against tuber transmission. Similar conclusions were reported by Orton and Hill (*19*) in 1938 and by Beall and Cannon (*1*) in 1946..

After it was shown that the disease was caused by the aster-yellows virus, tubers from plants artificially inoculated with the virus were saved and planted. Plants grown in the greenhouse or in cages outside and artificially inoculated with yellows usually died without forming tubers or formed only very small ones. In all only five tubers were thus obtained from which seven plants were grown. Although the resulting plants were small and lacked vigor, they showed none of the symptoms of purple-top wilt.

It can only be concluded from these experiments that the *virus does not survive long in the potato plant*. Why it does not survive and what happens to it is not known. This relationship is unique inasmuch as no other virus affecting the potato plant is known to behave in this way, unless it is the virus of sugar-beet curly top. The curly-top virus is known to affect potatoes in regions where the beet leafhopper is prevalent, but it has never been shown to be tuber-transmitted and it has never been reported on potatoes outside the region where the beet leafhoppers are present. It would be of interest to determine definitely whether the curly-top-virus is tuber-transmitted or whether it, like the aster-yellows virus, does not survive in the potato.

PATHOLOGICAL HISTOLOGY

The abnormal histology of affected plants has been described in considerable detail by Orton and Hill (*18*) and by Hill and Orton (*5*). These descriptions are not repeated here. Only those abnormalities considered to be of special diagnostic value will be discussed.

Necrosis of the phloem tissues appears to be one of the earliest tissue changes to be observed. With the degeneration of the phloem, translocation is inhibited, and elaborated food materials accumulate in the leaves and stems. All other tissue changes appear to follow the collapse of the phloem and probably are directly or indirectly caused by it.

Necrotic phloem appears at the base of the stem but eventually may be found to some extent throughout the stem, in the leaf petioles, in the tubers, and even in the roots. It is discontinuous in its origin and in early stages may appear as elongate flecks of brown necrotic tissue. In later stages the necrosis of the phloem becomes continuous, especially at the base of the stem, and adjacent parenchyma tissues may also become necrotic.

The terminal leaves, which show the first macroscopic symptoms, undergo striking histological changes. Like most tissues affected with viruses, these leaves show signs of retarded development. The palisade cells fail to elongate normally and the usual large intercellular spaces are lacking. The spongy mesophyll also appears to be retarded, and the intercellular spaces are much smaller than normally. This retarded development is soon followed by degenerative changes within the protoplast. The chloroplasts undergo gradual disintegration, and the abnormally dense protoplasm of the palisade cells becomes granular in structure. Starch grains, numerous at first, disintegrate, often leaving a dark, amorphous residue.

Leaves that were fully formed before symptoms of the disease appeared show less striking changes. They first show abnormal accumulation of starch. Similar accumulations of starch are found in the stems especially just above the nodes. Starch accumulation is especially heavy near the nodes and in the base of the axillary shoots where leaves, in which starch has accumulated, may undergo degenerative changes similar to those observed in the apical leaves.

Sections of the necrotic lesions in the stem end of affected tubers show that the cells surrounding the necrotic cells are suberized and that most of the starch has disappeared from the adjoining storage parenchyma. The microchemical changes associated with these lesions have been described in detail by Hill and Orton (*5*).

EPIPHYTOLOGY OF PURPLE-TOP WILT

The recognition of the aster-yellows virus as the cause of purple-top wilt opens the way for a study of factors influencing development of the disease and of possible means of control. Inasmuch as the virus is known to be transmitted only by the aster leafhopper, it is important to know as much as possible about the movement of this insect in and out of potato fields.

The aster leafhoppers may overwinter either as adults or as eggs deposited in the leaves of grains or grasses. The latter method is the commoner, although in West Virginia a few adults have been caught in early spring (as early as April 7), when nymphs could not be found and when there had not been sufficient warm weather for the maturity of nymphs from overwintered eggs. These catches have been interpreted as overwintered adults, although complete proof and evidence of the relative importance of the two methods is lacking.

The leafhoppers breed on young grain and other species of plants. All evidence indicates that the potato plant is not a preferred host and that they rarely if ever breed on potatoes. Since the virus is not readily transmitted from potato to potato, infection must result from viruliferous leafhoppers that migrate to the potato field from some other plants. It becomes important then to know the source of the virus transmitted by the vector and the factors influencing the movement of the leafhoppers into potato fields.

THE DAILY MOVEMENT OF ASTER LEAFHOPPERS:—A preliminary report on the daily flight of the leafhoppers has been presented by Leach and Mullin (*13*). These studies have been continued, and records of the daily flight for five growing seasons have been obtained.

Theoretically the movement of the leafhoppers could be controlled by any of several factors. They could tend to move from maturing cereal crops and weeds to plants that are still green and succulent; or they could migrate as a result of overpopulation as new broods mature. Also, their movement could be controlled by an inherent tendency to migrate at a certain time of the year, as has been shown by Carter (*2*) for the beet leafhopper, the vector of the curly-top virus. It is also possible that the movement could be controlled almost entirely by environmental factors such as temperature and rainfall.

In the studies of leafhopper movement a light trap was used consisting of a 75-watt electric light bulb suspended over a 10-inch funnel leading to a fruit jar containing sodium cyanide (Fig. 13). The light was turned on at dark and off shortly after sunrise. The insects caught were sorted and counted daily. Except for the first two years, minimum

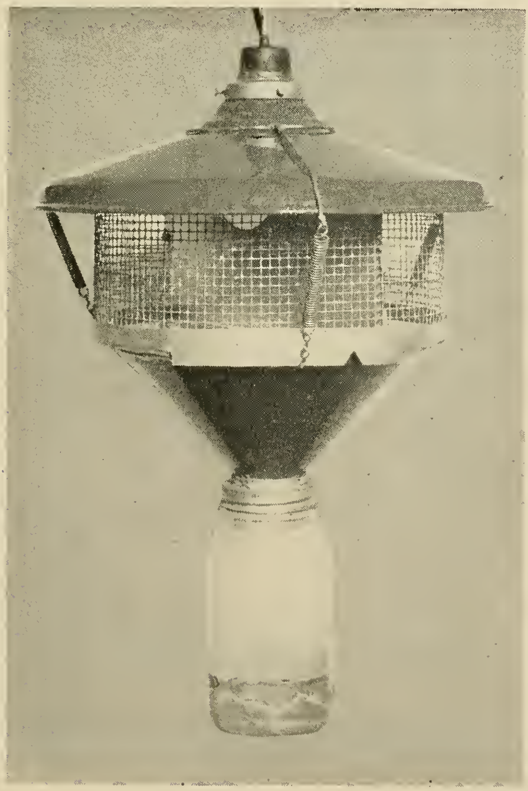

FIG. 13—Light trap used in the study of the movement of aster leafhoppers. The leafhoppers, attracted by the 75-watt electric light, entered the trap through the hardware cloth, were killed by the fumes of HCN, and collected in the jar attached to the funnel. The hardware cloth served to keep out larger insects and made it easier to count the leafhoppers carefully.

night temperatures were recorded at the trap, and the occurrence of rainfall during the night was noted.

Results of the five-year study on leafhopper movement show that the pattern of flight varied considerably from year to year. However, there is a fairly close correlation between the number of leafhoppers caught and the minimum daily temperature. The records for 1941 and 1942 are typical and will serve to illustrate the relationship (Fig. 14). In general, heavy flights occurred only when the minimum temperature was 60°F. or higher. Very few leafhoppers were caught on nights when the temperature fell below 60°. The greatest numbers were caught during a success-

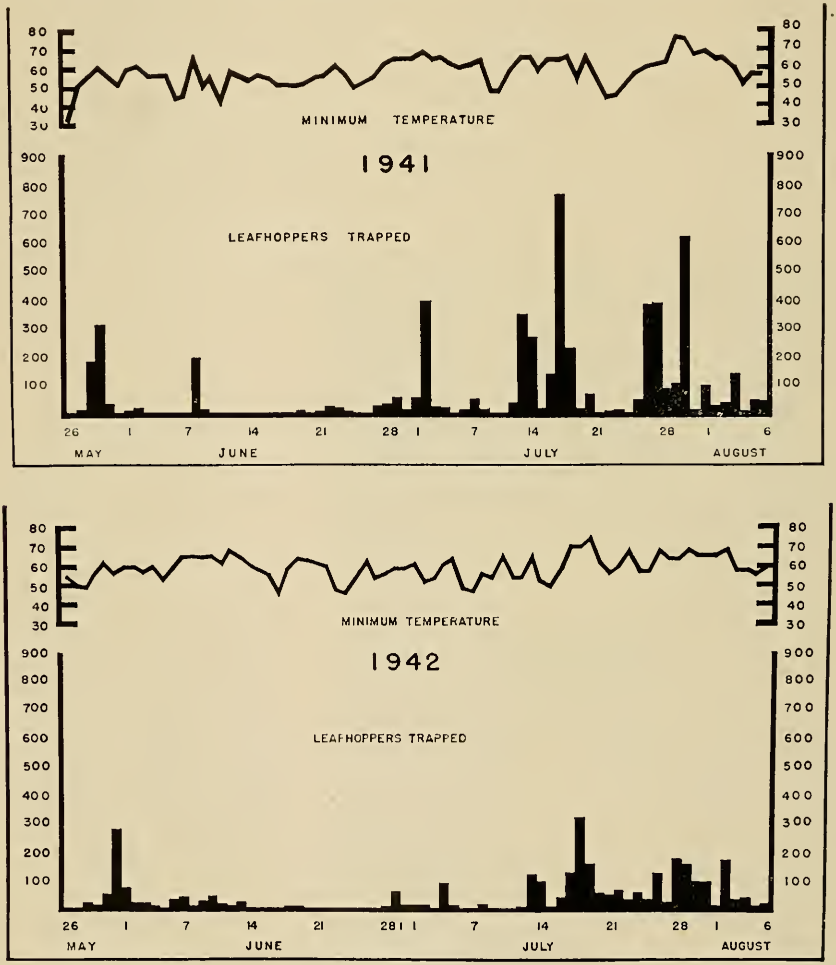

FIG. 14—Numbers of aster leafhoppers caught in light traps in relation to minimum daily temperatures in 1941 and 1942. The temperatures indicated are in degrees Fahrenheit.

ion of warm nights when the temperature did not fall below 60°. Occasionally there were nights when there were only a few insects caught although the temperature did not fall below 60°. In practically all cases this deviation was correlated with a light rainfall during the night that prevented the normal flight without depressing the temperature below 60°. These were the conditions occurring, for example, on July 31, 1941, and August 1, 1942, as shown in Figure 14.

In all probability there is no very close correlation between the movement of leafhoppers in daytime with that at night as determined by the light trap, but it can be safely concluded that, when large numbers are caught at night, the leafhoppers are present and probably also move during the day if conditions are favorable. Although in most years the larger flights occurred in midsummer or later, there was always a number of fairly heavy flights early in the season during May and the first part of June, and some movement probably occurs on warm days earlier in the season. It is believed that the hoppers of these early flights are, in all probability, the ones responsible for most of the inoculation of the potato crop. Because of the relatively long incubation period, those leafhoppers that move to potato fields *after midsummer* could not inoculate the plants early enough to result in symptoms before maturity of the crop.

It is not entirely clear how these leafhoppers become viruliferous. The commonest source of leafhoppers from overwintered eggs are winter cereals, as noted by Kunkel (*6*). The cereals, however, are immune to the virus, and insects from this source should not be viruliferous. It is possible that the earliest flight may be composed largely of overwintered adults, although proof is not available. If this is true, a greater proportion of viruliferous insects would be expected in the earlier flights. If the early flights do not include many overwintered adults, many of them must come from perennial plants affected with the virus. A few of such plants have been found, but they have not been observed in early spring in sufficient abundance to offer a satisfactory explanation.

The length of the incubation period in potatoes:—The incubation period of the virus in potato plants is relatively long. An average of 30 artificial inoculation experiments with viruliferous leafhoppers made at different times of the year gave incubation periods varying from 34 days to 68 days with an average of 49 days. This is considerably longer than the incubation period on asters as given by Kunkel (*6*) and as observed by the authors. The longest incubation periods occurred in midwinter, when light conditions were poor; the shortest ones were in early spring, when light conditions were better. The incubation period in the field would probably not be as long as that obtained in the greenhouse; all indications, however, are that it is at least five weeks or longer. This long period probably accounts for the fact that the disease does not appear on potatoes until relatively late in the season. The dates of the earliest symptoms observed in the experimental plots in West Virginia during the period of this study were as follows:

1939—July 17	1942—July 10
1940—July 16	1943—July 19
1941—July 17	1944—July 15

THE PROBABLE INFECTION PERIOD:—In an effort to obtain some information on the period of infection in nature, some cage experiments were made in 1943. Potatoes were planted in the field in 24 groups of 4 hills each. These were arranged in two series. In series 1 all 12 groups were covered with cages (4 plants to a cage) at time of planting. At weekly intervals, beginning June 11, as the plants were emerging, 2 of the cages were removed, exposing the plants to infection for the rest of the season. In series 2 the plants were left uncovered at planting time, but at weekly intervals, beginning June 11, 2 groups were covered with cages and left caged until the plants were mature. Notes were taken on the appearance of the disease in the various groups of plants. The results are given in Table 2 and are presented graphically in Fig. 15.

Although the number of plants involved in this experiment was relatively small, the disease was very prevalent in the field, averaging approximately 50 percent infection. The number of positive infections obtained was sufficient to give some indication of the probable time limits of infection. The data indicate that infection took place after June 11 and before July 9. None of the plants exposed until June 11 and kept covered thereafter became infected. None of the plants kept covered until July 9 and exposed thereafter developed symptoms of the disease. It is probable that some of the latter group may have been infected, but since the

Cage no.	Caged	Exposed	Infection
Series I			
1	June 4-11	June 11-	+
2	June 4-11	June 11-	+
3	June 4-18	June 18-	+
4	June 4-18	June 18-	+
5	June 4-25	June 25-	—
6	June 11-25	June 25-	+
7	June 4-July 2	July 2-	—
8	June 4-July 2	July 2-	+
9	June 4-July 9	July 9-	—
10	June 4-July 9	July 9-	—
11	June 4-July 16	July 16-	—
12	June 4-July 16	July 16-	—
Series II			
Cage no.	Caged	Exposed	Infection
13	June 11-	June 4-11	—
14	June 11-	June 4-11	—
15	June 18-	June 4-18	+
16	June 18-	June 4-18	+
17	June 25-	June 4-25	—
18	June 25-	June 4-25	—
19	July 2-	June 4-July 2	—
20	July 2-	June 4-July 2	+
21	July 9-	June 4-July 9	+
22	July 9-	June 4-July 9	+
23	July 16-	June 4-July 16	+
24	July 16-	June 4-July 16	+

TABLE 2—Occurrence of Purple-top Wilt on Potato Plants Caged for Different Periods of Time

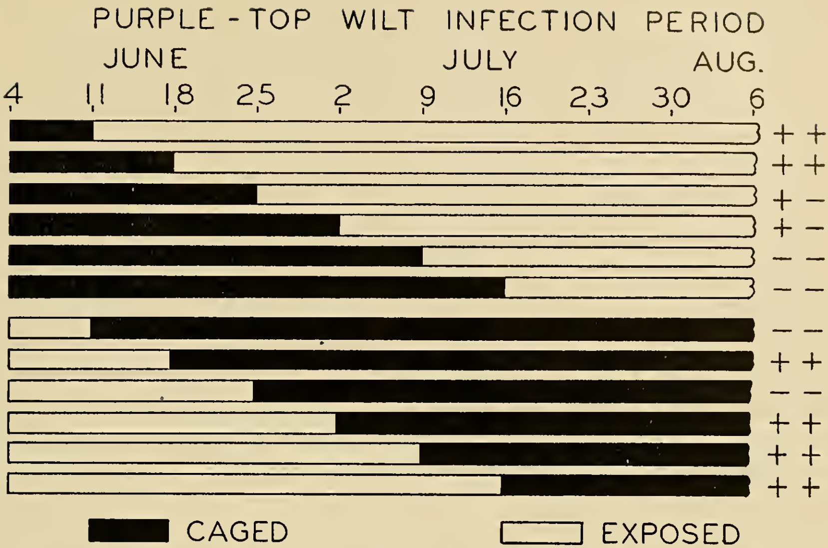

FIG. 15—Relationship of time of caging and time of exposure to infection of potatoes plants by purple-top wilt: "+" signifies infection; "—" signifies no infection in each of two cages.

disease has an incubation period of 5 weeks or longer, the infected plants probably matured before the symptoms could develop.

THE DISTRIBUTION OF INFECTED PLANTS IN A FIELD:—Since the aster leafhopper does not breed on potatoes, and since the virus is not tuber-transmitted and apparently cannot be transmitted readily from potato to potato, each infected plant must result from the feeding of a migratory adult leafhopper. In view of the relatively small number of aster leafhoppers observed in potato fields it is difficult, at first, to account for the high percentage of infection often found. However, it should be remembered that a single viruliferous leafhopper could inoculate several plants by feeding on each plant for a short time. Although the aster leafhoppers are, as a rule, not very active unless disturbed, they often do move from plant to plant of their own volition. Moreover, ordinary cultivating and spraying operations would cause them to move from one plant to another at frequent intervals.

It has been observed that purple-top wilt, although not confined to any particular part of a field, is rarely, if ever, evenly distributed. There are always small areas in which the percentage of infection is definitely higher than in similar adjacent areas. This has made it difficult to compare the relative susceptibility of varieties in small plots without excessive replication.

In an experimental plot of approximately one-fourth acre all the plants affected with purple-top wilt were marked as they were detected by careful inspection three times each week. An apparent tendency was observed for affected plants showing up late to be clustered about those marked during the first few weeks. This suggested that the first plants affected were serving as centers of infection. In an effort to test the accuracy of this observation a map was made of the field showing the positions of each diseased plant and the date of its appearance. It was reasoned that, if the apparent tendency of the diseased plants to be grouped about the earliest recorded ones was of any significance, it could be determined by comparing the number of diseased plants in 2 sets of comparable areas, one adjacent to, and the other separated from, the earliest infected plants. Therefore a number of the earliest-recorded diseased plants were selected. Those located in 2 rows of the edge of the field were eliminated as unsuitable for use because they could not permit a complete pattern of distribution. Also those recorded after August 9 were eliminated because plants after this date would probably not develop symptoms before maturity. This left a total of 49 plants or approximately one-sixth of the total number of diseased plants recorded. Using these plants as focal points, the number of diseased plants occurring in 16 adjacent plant positions were counted and compared with the number in the 32 immediately surrounding plant positions as shown in Figure 16. If the position of the diseased plants was due to chance distribution, the expected diseased

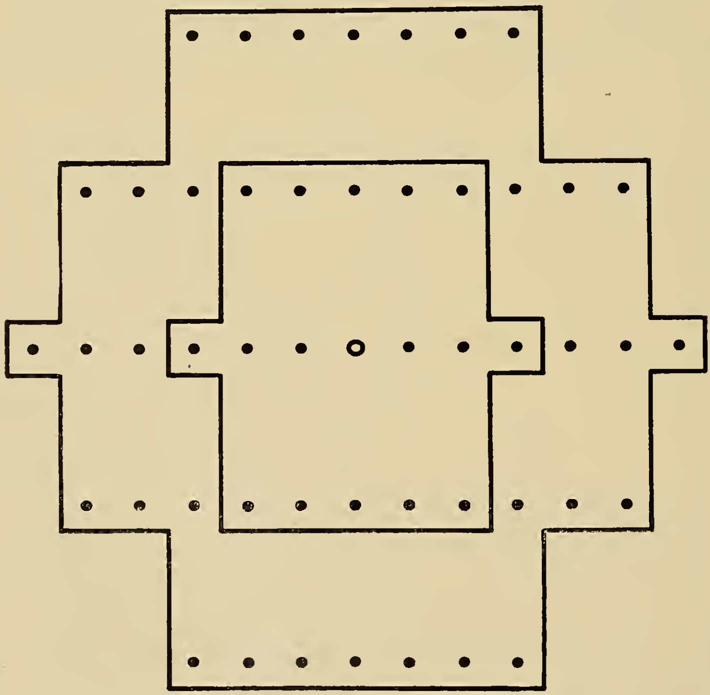

FIG. 16—Two zones mapped in relation to an early-infected plant and used in studying the distribution of affected plants showing up later in the season. The circle represents the early-infected plant and the dots the plant positions counted in the two zones.

plants in the 16 adjacent positions would be one-half as many as those occurring in the 32 more remote positions. The actual counts were 113 in the adjacent positions and 192 in the remote positions. The actual number of 113 is 17.8 percent in excess of the expected number of 96. This would indicate that the apparent tendency of the diseased plants to be grouped about the earliest ones infected was real and that the cluster of infected plants in each case is probably the result of the activity of a *single viruliferous leafhopper.*

THE CONTROL OF PURPLE-TOP WILT

No satisfactory method of controlling purple-top wilt is known. Since the disease is not perpetuated in the tubers, roguing out diseased plants has no value as a control measure; and no dependence can be placed on the use of certified seed. In West Virginia some loss from the disease may be avoided by planting early varieties, such as the Irish Cobbler, that mature early enough to escape the disease. This control measure, however, is not effective in all sections of the country and it is not practical at the higher altitudes in West Virginia, where other varieties are better adapted.

Since plants grown in screen-wire or aster-cloth cages never contract the disease, it is safe to assume that effective control could be obtained by growing potatoes, like asters, under aster-cloth tents, but the expense of such a method makes it impractical for potatoes.

If it were possible to protect potato plants from the aster leafhopper by means of an insecticidal spray or dust, a practical method of control might be devised. Spraying with Bordeaux mixture has given partial control of the potato leafhopper by preventing the building up of large populations of the insect. Spraying potatoes with Bordeaux mixture, however, has little effect on the aster leafhopper and on purple-top wilt, since this insect does not breed *on the potato,* and its injury is not dependent upon the building up of large populations. Numerous counts and observations have revealed no significant control of purple-top wilt by spraying with Bordeaux mixture.

The striking effectiveness of DDT in the control of the potato leafhopper suggests that it might be of some value in the control of purple-top wilt by shortening the life of the adult aster leafhoppers that migrate to potato fields. With the view of obtaining some information on the question, notes were taken on the prevalence of purple-top wilt in the plots of a potato-spray experiment in which DDT was used. The experiment included the following sprays and spray combinations:

(1) Bordeaux mixture (2) Bordeaux mixture plus DDT (3/4 lb. to 100 gal.), (3) DDT alone, (4) dithane, (5) dithane plus DDT, and (6) unsprayed check. Each plot consisted of 4 rows 60 feet in length; notes were taken on the 2 center rows.

A high degree of control of potato leafhoppers was obtained on the DDT plots, but the influence of DDT on the leafhoppers had extended to the adjacent plots to such an extent that good control was obtained also on plots receiving no DDT. This effect was apparent also on the control of aster leafhoppers. Although there was some indication of the control of aster leafhoppers by DDT, the differences were so small that they are not considered significant. Notes were taken also on the purple-top wilt in all plots except the check plot and the one receiving DDT only, the plants in these having been killed by late blight before purple-top wilt had developed sufficiently for note-taking. The differences were not significant. The data are given in Table 3.

TABLE 3—Effect of DDT on Control of Leafhoppers and Purple-top Wilt on Potatoes in 4-row Adjacent Spray Plots

Spray	Potato leaf-hoppers(a)	Aster leaf-hoppers(a)	Purple-top wilt (b)
Bordeaux mixture 8-8-100			
Rep. 1	241	8	12
Rep. 2	90	8	14
Rep. 3	98	7	17
Rep. 4	119	10	5
Bordeaux mixture plus DDT			
Rep. 1	9	1	14
Rep. 2	7	2	7
Rep. 3	6	5	13
Rep. 4	6	3	8
DDT only			
Rep. 1	5	4	(d)
Rep. 2	18	1	
Rep. 3	9	2	
Rep. 4	17	2	
Dithane only			
Rep. 1	91	5	8
Rep. 2	112	7	6
Rep. 3	85	5	5
Rep. 4	90	12	11
Dithane Plus DDT			
Rep. 1	19	4	4
Rep. 2	9	1	9
Rep. 3	11	2	14
Rep. 4	4	1	8
Check			
Rep. 1	98	5	(d)
Rep. 2	89	3	
Isolated check (c)	1000+	14	

(a) Number caught in 50 sweeps with a net over 2 center rows—July 28.
(b) Notes taken August 23.
(c) Plot of same variety planted same date separated by 12 rows of corn.
(d) Disease obscured by late blight infection.

Better evidence that DDT may have some value in the control of purple-top wilt was obtained from a dusting experiment in which DDT dust was compared with copperlime dust. A rectanglar plot of approximately one-fifth acre was divided in half at right angles to the long axis and to the row direction. One-half of the plot was dusted with 20-80 copperlime dust and the other half with a 5 percent DDT dust in pyrophyllite. Eight applications were made at intervals of approximately one week, the dusts being applied with crank dusters. In this experiment the effect of the DDT apparently did not extend very far into the copper-lime-dust plot, and there was a fairly sharp line of demarcation between the plots as shown by the control of hopper burn on the DDT plot.

Counts of purple-top wilt in the plots were made on two dates: August 13 and August 20. Since the prevalence of the disease increases until maturity of the crop, a third count was planned but could not be taken because of heavy late-blight infection that developed in the plot about September 10.

Leafhopper counts were made on the day on which notes on purple-top wilt were taken. One hundred sweeps of the net were made over each plot. The insects were killed with cyanide gas before counting. The data are given in Table 4.

In this experiment, where the plots were larger and were end to end, the carryover effect of DDT was not sufficient to obscure the differences in leafhopper control. There was significant control of both kinds of leafhoppers, and there was definitely less purple-top wilt in the plot dusted with DDT.

TABLE 4—Effect of DDT Dust and Copper-lime Dust on Control of Leafhoppers and Purple-top Wilt in Single Unreplicated 1/10-acre Plots

Dust	Potato leaf-hoppers (a)		Aster leaf-hoppers (a)		Purple-top wilt	
	Aug. 13	Aug. 20	Aug. 13	Aug. 20	Aug. 13	Aug. 20
Copper lime (20-80)	633	528	9	26	39	58
DDT 5%	16	41	4	4	6	

(a) Number caught in 100 sweeps of the net.

These experiments, although preliminary in nature and not very extensive, indicate that some degree of control of aster leafhoppers on potatoes may be expected from DDT, which apparently shortens the life of migratory adults. Further work must be done before any definite statements can be made as to the value of DDT in controlling purple-top wilt, but it seems reasonable to believe that if DDT is extensively used on potatoes, some degree of protection against purple-top wilt may be expected.

Purple-top wilt in relation to seed certification:—Since purple-top wilt is not tuber-transmitted, it is obvious that it cannot be eliminated through seed certification. This does not mean, however, that the disease can be ignored in certification practice. Whether specific tolerances for purple-top wilt should be included in certification requirements, and if so, how much should be allowed, are pertinent questions. If tolerance limitations are considered solely from the standpoint of controlling the disease as for mosaic, leaf roll, and other tuber-transmitted diseases, there is no justification for tolerance limitations. However, observations show that tubers from affected plants produce weaker plants than tubers from healthy plants. Comparative yield tests made in West Virginia with carefully selected tubers planted in adjacent rows in 1943 and in 1945 resulted in reduced yields of 27.3 percent and 21.5 percent respectively, or an average of 24.4 percent. Obviously, then, plants affected with purple-top wilt do not produce tubers of high seed value. It can be calculated that the seedstock from a field with 100 percent purple-top wilt would have a yielding value of about 24 percent less than seed from a field with no purple-top wilt, other things being equal. It might be concluded that a field with 50 percent infected plants would suffer a 12-percent reduction in yielding value, but this figure would be correct only if the plants affected with purple-top wilt produced as much as healthy ones. It is important then to know how much current season reduction in yield may be expected from affected plants.

As previously stated, it can be observed readily that the reduction in yield depends somewhat upon the time of infection, those infected earlier yielding less than those becoming infected late in the season. In order to measure the reduction more accurately, the plants in a small field were examined 3 times each week, and all diseased plants were marked with a numbered stake as soon as symptoms appeared. The first plant was marked on July 21, and by the 29th of August, when plant maturity made it difficult to recognize symptoms, 291 diseased plants had been marked. On this date 100 obviously healthy ones were marked. Two weeks later the marked hills were harvested individually and weighed. The data tabulated for different groups of plants on the basis of date of first symptoms are given in Table 5. The average yield per hill for the diseased plants was 7.77 ounces compared with an average yield of 16.82 ounces for the 100 healthy plants. The data show that diseased plants on the average yield slightly less than one-half as much as healthy ones and that those affected early yielded less than those affected later.

Taking this fact into consideration, it can be seen that with 50 percent affected plants there would be only one-half as much weak seed as normal seed, and this would reduce the yielding value of the seedlot not more than eight percent. But a yielding value 8 percent below normal should not be permitted in certified seed. In the same way it can be calculated that the yielding value of seed from a field with 25 percent infection would be reduced approximately 3.5 percent, and that from a field with 10 percent infection, 1.25 percent.

Where, then, should the tolerance limit be set? The tolerance of the reduced yielding value would have to be set arbitrarily, but the percentage of infection allowed in field inspections necessary to meet a given tolerance would depend on the date of field inspection, because the disease increases progressively until the plants mature. Should a tolerance limit be established, the last field inspection should be made as late as possible and, if there is much variation in this respect, the tolerance limit should

TABLE 5—Effect of Purple-top Wilt on Yield

Date of first symptoms	No. of plants	Yield in oz. per plant
7/21 to 8/9	68	5.28
8/9 to 8/27	223	8.53
8/18 to 8/27	148	8.64
7/21 to 8/27	291	7.77
Healthy plants	100	16.82

be flexible, so that a lower limit could be used for inspections made early. Since the disease does not spread from potato plant to potato plant in the field, it would be permissible to meet any tolerance limit by roguing out affected plants, no matter how high the percentage of infection or how late the roguing is done, provided the tubers are removed with the plant.

From the standpoint of certification practice, purple-top wilt should be viewed more as a weak plant than as an infectious virus disease; and if tolerance limit is adopted, it should be relatively high. All the evidence indicates that a tolerance of 10 to 20 percent purple-top wilt would be less dangerous than a tolerance of 1 to 2 percent for such virus diseases as leaf roll, rugose, mosaic, or spindle tuber.

It should be remembered that the evidence for the above conclusions is based on West Virginia conditions. The effects of the disease on immediate yield and on yield of the subsequent crop should be determined in the regions where certified seed is grown, and final regulations should be formulated on the basis of local conditions.

SUMMARY

1. The known facts about a disease of potatoes known as purple-top wilt (also known as blue stem) are reviewed, and the results of studies on the disease in West Virginia since 1939 are given.
2. The symptoms of the disease are described and compared with those of similar diseases with which purple-top wilt has been confused.
3. Evidence is presented to show that the disease is caused by the aster-yellows virus and is transmitted to potatoes by the aster leafhopper, *Macrosteles divisus* (Uhl.).
4. Potato plants grown under cages of screen wire or aster cloth do not contract the disease unless viruliferous aster leafhoppers are introduced.
5. The symptoms produced on potatoes by artificial inoculation with the aster-yellows virus are similar but not identical with those occurring on potatoes in nature. The differences, however, are minor and are attributed to reduced light intensity and to other abnormal conditions in the greenhouse and under cages that result in reduced photosynthetic activity.
6. All efforts to transmit the virus from potatoes to asters or from potatoes to potatoes by means of leafhoppers have failed. This was true both with naturally affected plants and with those artificially inoculated with the virus by viruliferous leafhoppers.
7. Efforts to transmit the virus from potatoes to potatoes or from potatoes to *Nicotiana rustica* by grafting have failed.
8. All efforts to perpetuate the virus in potato plants by making cuttings from affected plants have failed because such cuttings did not take root, while similar cuttings from healthy plants were rooted successfully.
9. The virus is not perpetuated in potato tubers from affected plants. This is true for both naturally infected plants and those artificially inoculated with the virus from asters.

10. The incubation period of the virus in potatoes is longer than it is in asters and some other plants. It varied in cage experiments from 34 to 68 days, with an average of 49 days.
11. Cage experiments in which potato plants were exposed at different intervals during the season indicate that field infection probably occurs relatively early in the season, probably after June 11 and before July 9.
12. No evidence was found to support the theory that "hair sprout" is the result of purple-top wilt infection of the plant on which the "hair sprout" tubers were produced.
13. Comparative yield tests indicate that plants affected with purple-top wilt yield, on the average, slightly less than one-half as much as healthy plants. Plants that do not show symptoms until late in the season yield more than those affected early.
14. The daily mass movement of aster leafhoppers was studied with the aid of a light trap. The minimum daily temperature appeared to be the principal factor controlling leafhopper movement. There was little movement and few leafhoppers were caught when the minimum temperature was 60° F. or lower. There were two or more periods of heavy flight during each summer, but there was always a number of fairly heavy flights during May and early June. Evidence indicates that the hoppers of these early flights are the ones responsible for infection of potatoes. It is not known definitely how these leafhoppers become viruliferous, probably from feeding on infected perennial weeds, but some of them may be overwintered viruliferous adults. Some circumstantial evidence has been obtained indicating that there is some overwintering of adults in West Virginia, but it apparently is not very extensive.
15. There is no evidence that aster leafhoppers breed on potatoes: and the virus does not spread from potato to potato. Therefore infection on potatoes must arise from migratory adult leafhoppers. A tendency for first plants showing infection to act as centers of infection resulting in groups of infected plants can probably be explained by the movements of individual migratory viruliferous leafhoppers.
16. No satisfactory control measure for purple-top wilt is yet available, although there is some evidence that the amount of infection can be reduced by dusting or spraying the plants with DDT. It is believed that this reduction in infection may be due to a shortening of the life of adult aster leafhoppers on potatoes, thus reducing the number of plants inoculated.
17. The relation of purple-top wilt to potato seed-certification practices is discussed. If purple-top wilt tolerance limits are established, they should be based on the behavior of the affected plants as weak plants rather than as plants affected with an infectious virus disease such as leaf roll, rugose mosaic, etc. Tolerances, if established, should be liberal and should be flexible to allow for differences in date of inspection. Roguing should be permitted to meet the tolerances, and field inspections should be made as late in the season as possible.

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